# Temperature variability and fluctuation in the humus layer of a temperate deciduous forest in spring: implications on the resident fauna

A. Bruckner

# Temperaturverhältnisse im Lebensraum der humusbewohnenden Fauna eines temperaten Laubwaldes im Frühling

## 1. Introduction

In most temperate forests, the mineral soil is permanently covered with fresh or partly decomposed dead organic matter. Most soil organisms dwell in these humus layers. A range of biotic and abiotic factors determines their distribution, activity, and contribution to decomposition and nutrient cycling. Among the abiotic factors, temperature and moisture are of primary importance. For example, BERG et al. (1998) found that the abundance of several arthropod groups in pine humus can be explained by these factors in a multiple regression analysis. The body surface of many forest soil animals is more or less permeable for water. Thus, they generally prefer high moisture and low temperature levels and are less sensitive to low than to high temperatures (KILLHAM, 1994; TOPP, 1981). If conditions in litter become severe, animals retreat to deeper humus or soil strata to avoid overheating and desiccation. Forest litter layers reduce the diurnal and seasonal temperature oscillations of bare soil (BALISKY and BURTON, 1995; FRANSSILA, 1960). From a biological point of view, the forest floor can be expected to provide a stable and predictable habitat for animals.

Despite a considerable body of literature on temperature patterns of the mineral soil, no such data exist for forest floor humus. This is surprising in view of the paramount importance of this factor for soil biota and tree seedling establishment (MCINNIS and ROBERTS, 1995; SPITTLEHOUSE and STATHERS, 1990). Temperature patterns of the forest floor are not easily predicted due to great spatial and temporal variability of governing factors, especially moisture, humus thickness, vegetation, and air temperature (BALISKY and BURTON, 1995; CHEN and FRANKLIN, 1997; CLARK et al., 1995; HOKKANEN et al., 1995; XU et al., 1997). Thus, more detailed examination is necessary for a proper understanding of the temperature environment of


### Zusammenfassung

Die Temperaturverhältnisse im Auflagehumus eines kühl-temperaten Buchenwaldes im Frühling wurden untersucht. An klaren Tagen vor Austreiben der Knospen erreichten die Temperaturen des L-Horizonts 20–40° C, bedingt durch hohe direkte Einstrahlung durch die unbelaubten Baumkronen. Die diurnalen und die kurzzeitigen Temperaturschwankungen waren sehr hoch, mit extremen Unterschieden von 13,0 bis 18,5° C innerhalb 5 bis 15 Minuten. Nach der Blattentfaltung waren die Schwankungen im L-Horizont gedämpft und die Temperaturen überschritten 25° C kaum. F- und $A_h$-Horizont waren während des gesamten Untersuchungszeitraums viel kühler und feuchter als der L-Horizont, mit geringen diurnalen und kurzzeitigen Schwankungen. Die Temperaturen und die Temperaturschwankungen im F- und $A_h$-Horizont waren sehr ähnlich und weitgehend unabhängig von der Tiefe im Profil. Die horizontale Variabilität der Temperatur an der F / $A_h$- Grenze zwischen unterschiedlichen Mikro-Standorten war gering. Der L-Horizont temperater Laubwälder dürfte daher eine lebensfeindliche und unvorhersehbare Umgebung für zarthäutige Bodentiere sein. Dagegen sind im Frühjahr die Bedingungen in den tieferen Horizonten kühl, feucht und sehr stabil.


**Schlagworte:** Bodenökologie, Bodenfauna, Humushorizont, Variabilität.

**Summary**

The temperature of forest floor humus during spring was studied in a cool-temperate beech stand. Before bud break, temperatures in the L horizon peaked at 20–40° C on clear days due to high insulation through the open canopy. Diurnal and short-term variability were very high, with extreme shifts of up to 13.0 to 18.5° C within a 5 to 15 minute span. After leaf expansion, temperature fluctuations were greatly reduced in the L horizon and temperatures rarely exceeded 25° C. The F and $A_h$ horizons were much cooler and wetter than the L horizon, exhibiting minimal diurnal and short-term variability during the entire study. Temperatures and the temporal temperature variability in the F and $A_h$ horizons were always very similar and were largely independent of depth. The spatial variability of temperature at the F – $A_h$ boundary between different microsites was low. The L horizon of temperate deciduous forests can therefore be a hostile and unpredictable environment for humus-dwelling animals. In contrast, conditions in the deeper horizons are cool, moist and very stable, and therefore are more favorable to the resident fauna.

**Key words:** soil ecology, soil fauna, humus stratification, variability.

humus inhabitants. As a preliminary study, I chose an extreme case: humus temperature in spring.

During the spring season (March to May), the floor of cool-temperate deciduous forests receives a great proportion of the year's total radiation. Solar altitude increases rapidly in this time and only bare tree branches and stems intercept incoming radiation. A substantial portion of the light arrives at high flux densities (beam radiation). As the leaves expand (mid-April to mid-May), light is rapidly attenuated with increasing leaf area and pigmentation, despite still increasing total radiation incident upon the forest canopy. Diffuse light dominates inside the forest. Beam radiation occurs mainly in form of ephemeral sunflecks penetrating through canopy openings. Light conditions at ground level in this "summer shade phase" remain steady until the onset of leaf abscission in autumn (ANDERSON, 1964; BALDOCCHI et al., 1984; HUTCHISON and MATT, 1977).

The botanist FIRBAS (1927) discovered that high light intensities at the woodland floor in spring coincide with elevated surface temperatures. He found that incoming radiation heats up litter and air above the ground, thus allowing thermophilic geophytes to grow and reproduce in a short time. Accordingly, surface temperatures of 25–30° C are common during clear days in late April and early May, and 40° C are "not rare". However, the soil beneath the humus remains cool. Short-term temperature fluctuations are high and the litter rapidly cools in the evening and at night. Once the trees are in leaf, fluctuations are smoother and extremes rarely occur.

What are the implications of these findings on the ecology of humus-dwelling animals? Does the forest floor in spring really provide stable and predictable conditions, as generally expected? If not: do animals have a retreat when surface conditions become adverse? In order to answer these questions, I designed an investigation with the following objectives: (1) to elaborate Firbas' 1927 findings with modern meteorological equipment; (2) to characterize the influence of canopy leafiness on humus temperature; (3) to examine the vertical temperature gradient in the humus profile; and (4) to characterize the spatial variability of the temperature environment at the forest stand level.

## 2. Materials and Methods

### 2.1 Study site

The study site was situated at the "Gelber Berg" in Purkersdorf, Lower Austria (16° 11'E, 48° 12'N, 430 m above sea level) on a steep (20–25°), south-facing slope. A 90x114 m, mature forest stand was chosen for the measurement. The tree cover was uniform and consisted of an even-aged, single layer of beech (*Fagus sylvatica,* 87 % dominance) and oak (*Quercus petraea,* 13 %). Average minimum distance between trees was 2.8 m (8.3 stems.100 $m^{-2}$) and tree height was about 30 m. A shrub layer had not developed. The estimated total ground coverage of herbs was 3 %. The humus form was best characterized as a Leptomoder (GREEN et al., 1993), but without a distinct H horizon (tab. 1), which has developoed on a sandy loam.

Mean annual temperature and precipitation of the region are 9.4° C and 642 mm, respectively, with 33 % of annual precipitation falling during the summer months.

Table 1: Characteristics of humus horizons at the study site according to GREEN et al. (1993)
Tabelle 1: Beschreibung der Humushorizonte der Untersuchungsfläche nach GREEN et al. (1993)

| horizon | characteristics |
|---|---|
| Ln | thickness 0-30mm; loose, intact beech and oak leaves; mostly desiccated |
| Fz1 | thickness 20-30mm; partly decomposed leaves; weakly to moderately matted; moist to wet; few fine roots |
| Fz2 | thickness 0-30mm; partly decomposed leaves; not or weakly matted; moist to wet; common to plentiful fine roots |
| $A_h$ | thickness 0-20mm; abundant faunal droppings; moist to wet; common fine roots |

The dominant beech came into leaf during a warm period in late April. First signs of bud break were detected in the crowns on Julian day 102 (April 12), and the canopy leaves appeared fully expanded from day 116 (April 26) onwards.

## 2.2 Experimental protocol

Temperatures were determined in April and May, 1998. Copper-constantan thermocouples were installed in litter and soil horizons of a humus/soil profile (tab. 2) from April 9 (day 99) to May 18 (day 138). One thermocouple was positioned 30mm above the litter surface. A Campell Scientific CR10 datalogger was programmed to record data from each thermocouple every minute. Two periods were selected for further data analysis: days 100-111 (before bud break), and days 126–137 (with canopy leaves expanded).

Additionally, 12 automatic temperature dataloggers (Tinytag, Gemini Data Loggers, UK) were exposed in the humus on April 3, 1998 (day 93). The points were selected as to represent microsites of increasing humus thickness (ranging from a shallow litter cover at a wind-blown ridge to thick heaps of litter accumulated by the sedge *Carex pendula* or by down logs). Temperature was measured at the bases of the humus profiles (at the boundary of F and $A_h$ horizons) every 5 minutes. On April 29 (day 119), the sensors were removed, offloaded, and exposed in the same positions from May 1 (day 121) to 28 (day 148). To avoid radiation heating of the Tinytags, all sensors were completely covered by a > 20 mm layer of leaves. Three Tinytags were repeatedly found blown free. These measurements had to be removed from the data set, so subsequent analyses were based on a sample of 9 Tinytags.

Weather data were obtained from a meteorological station nearby (Hohe Warte, Zentralanstalt für Meteorologie und Geodynamik).

## 2.3 Statistical treatment of data

For data analysis, nonparametric statistics (medians, percentiles, Kruskal-Wallis test) and graphical methods were preferred because data and experimental setup were often not conforming to the assumptions of normality and independence of observations, respectively.

# 3. Results

## 3.1 Temperature profile

On clear days before the trees came into leaf, temperatures of the L horizon (and, to a lesser extent, of the middle L horizon) exhibited a pronounced day-night cycle (fig. 1a) and were closely related to air temperatures 30 mm above the surface. Daytime temperatures of the L horizon frequently and abruptly rose to high peaks (20–40° C) of short duration, thus producing a jagged appearance of the plot

Table 2: Positions of thermocouples in the measurement profile. Values in mm refer to distance from the boundary between F (humus) and $A_h$ (mineral soil)
Tabelle 2: Positionen der Thermofühler im Profil. Werte in mm beziehen sich auf den Abstand zur Grenze zwischen F- (Humus) und $A_h$-(Mineralboden) Horizont

| position in profile | description |
|---|---|
| air | 30mm above the litter surface, recorded air temperature above the ground |
| + 65 mm | under two beech leaves, loosely fixed in place with florist wire |
| + 60 mm | in the middle of the L layer |
| + 40 mm | in a sparsely rooted sub-layer of the F horizon |
| + 25 mm | in a densely rooted sub-layer of the F horizon |
| ± 0 mm | at the F – $A_h$ boundary |
| - 50 mm | in the mineral soil |

(fig. 1a). The short-term fluctuations appear purely random at first sight. However, the sharp temperature drops between the peaks always occurred at the same time of day. This regularity may be attributed to shading by tree stems and large branches. Temperatures at night were less variable than during the day and decreased below the levels of the lower horizons on cold nights and after precipitation.

In sharp contrast, temporal temperature variability of both F and $A_h$ horizons was small (fig. 1a). The temperature fluctuations of the air and L horizon were also evident in these deeper strata, but with exceedingly reduced amplitude.

On clear days after leaf expansion, the air and L horizon again exhibited a common and distinct temperature regime (fig. 1b). However, diurnal and short-term fluctuations were much smoother than before the bud break and temperatures rarely exceeded 25° C. Three short-term peaks regularly appeared during daytime, most probably as a result of sunflecks. Similar to the leafless period, the temperatures of the lower layers did not differ substantially from each other and exhibited comparatively minor diurnal oscillations.

On overcast days of both periods, the temperature fluctuations of the L horizon were damped and extremes did not occur (fig. 1c, d). There was no great contrast between the temperatures of L and lower layers. Again, L temperatures closely followed those of the air. The behavior of deeper horizons did not differ much from sunny days.

Overall temperature variability (calculated separately for each measurement period) was small for the deeper strata

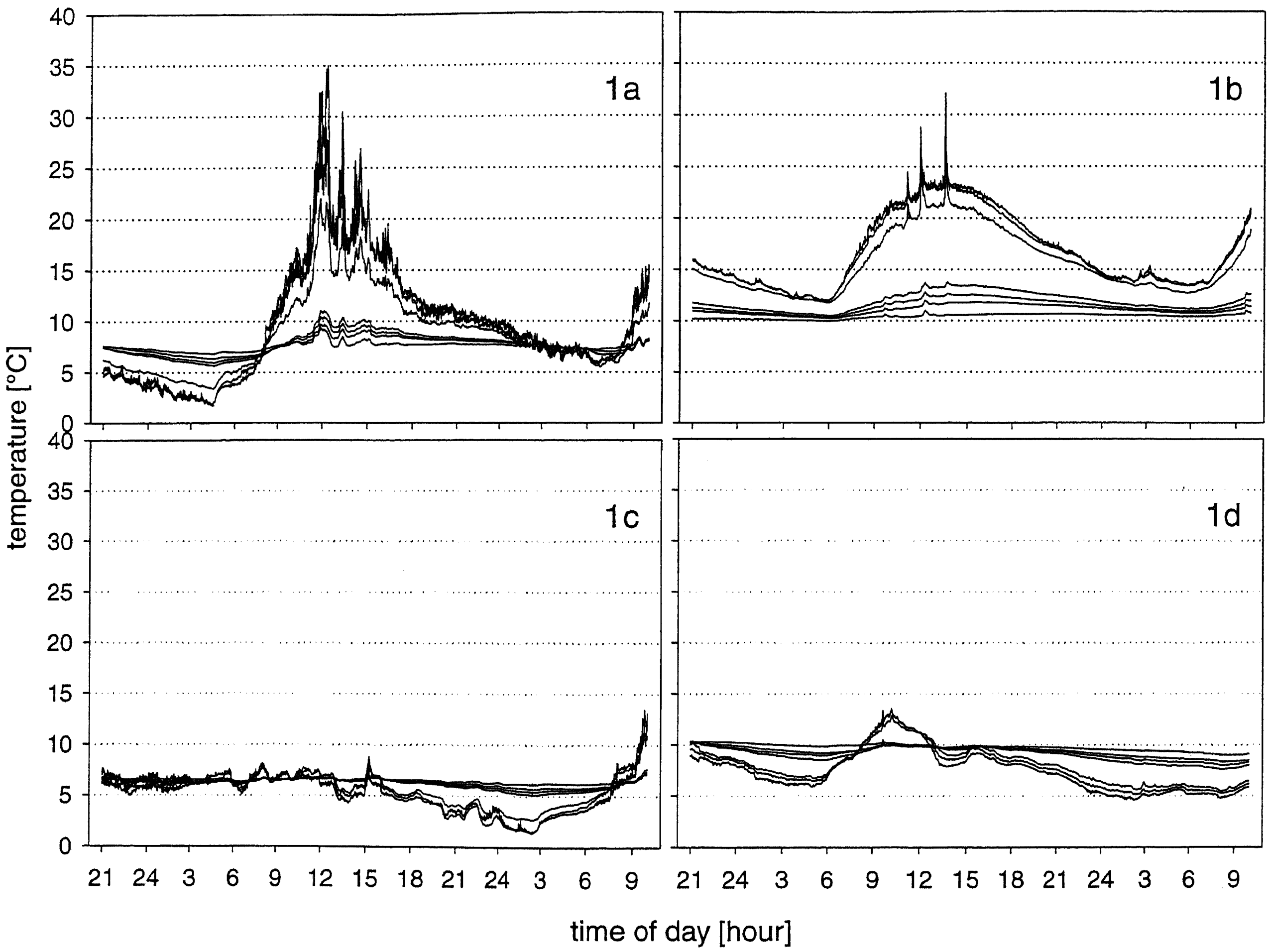


Figure 1: Humus temperatures of representative days before (a,c) and after (b,d) trees came into leaf. The heavily fluctuating lines represent air and L layer temperatures, the smoother lines the deeper layers. (a) day 100: open sky and sunny, following mild weather, (b) day 129: open sky and sunny, following mild weather, (c) day 106: cloudy sky throughout, 7mm precipitation, (d) day 136: following a dry and warm period, cloudy sky from late morning onwards, 1mm precipitation

Abbildung 1: Humustemperaturen repräsentativer Tage vor (a,c) und nach (b,d) der Blattentfaltung. Die stark fluktuierenden Linien repräsentieren die Temperaturen der Luft und des L-Horizonts, die glatteren Linien die der tieferen Horizonte. (a) Tag 100 war klar und sonnig, folgte auf mildes Wetter, (b) Tag 129 war klar und sonnig, folgte auf mildes Wetter, (c) Tag 106 war bewölkt mit 7mm Niederschlag, (d) Tag 136 war ab dem späten Vormittag bewölkt mit 1mm Niederschlag, folgte auf trocken-warme Periode and did not differ considerably between layers (fig. 2a, b). Above the F horizon, variability increased sharply and exceeded that of deeper layers 3 to 5 times. Temperature variability was about the same for both measurement periods, except for a few extremes prior to bud break, which greatly increased the temperature range of that period. A general warming of all strata was evident from April to May.

To characterize the change of temperature with time, the absolute difference $\Delta T$ [° C] between successive measurements was calculated for each sampling depth at 5, 15, 30, and 60 minute intervals over the two measurement periods (tab. 3, 4). In the L horizon, most temporal variability was in the range of 2-3° C, but extreme temperature shifts of up to 13.0-18.5° C occurred even within the 5 to 15 minute intervals. In general, $\Delta T$ of the L horizon was smaller after than before leaf expansion. Nevertheless, the maxima reached 13.6° C when trees were in leaf. In contrast, temporal variability was very small in deeper layers during both measurement periods and, within 5 to 60 minutes, no extremes exceeding 2.5° C were recorded here. Medians and interquartile ranges of $\Delta T$ increased with time interval. This was not true for high values (> 90 % percentile) in the L horizon: they were essentially in the same range from the 5 to the 60 minute interval. This again reflects the occurrence of extremely short-term temperature fluctuations during the day due to stem shading (before bud break) and sunflecks (when trees were in leaf).

Median temporal variability of the air (30mm above litter surface) and litter surface was similar in both periods (tab. 3, 4). However, 90 % percentile and especially the maxima were up to two times higher on the litter surface. Thus, great and rapid shifts of temperature are more frequent in litter than in the air body above.

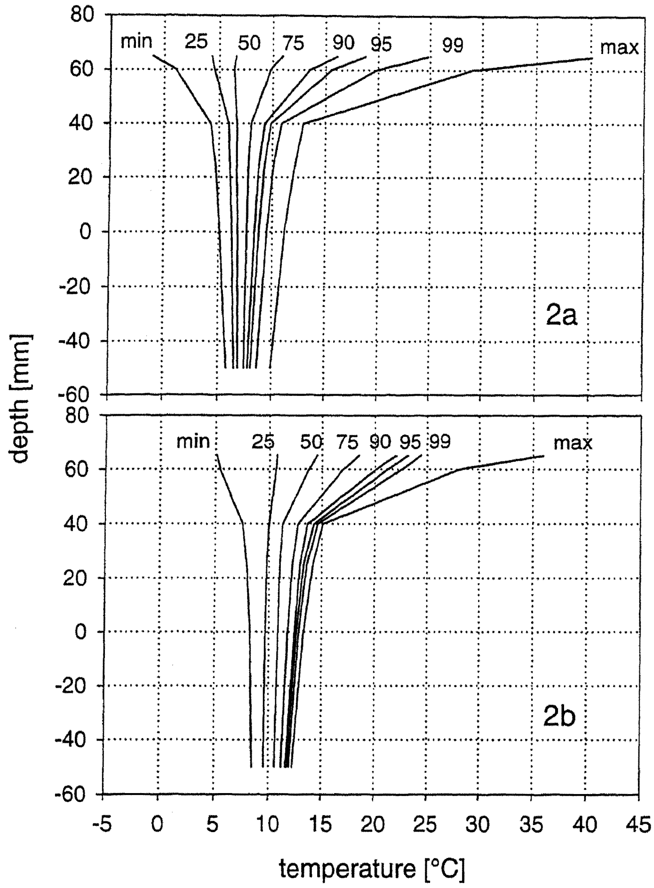


Figure 2: Vertical profile of temperature variability before (a, days 100–111) and after (b, days 126–137) trees came into leaf. Top values are percentiles, minimum and maximum

Abbildung 2: Vertikalprofil der Temperatur-Variabilität vor (a, Tag 100–111) und nach (b, Tag 126–137) der Blattentfaltung. Die Zahlen sind Perzentile, Minimum und Maximum

Table 3: Absolute temperature difference $\Delta T$ between successive measurements before bud break (days 100–111). Columns of table are time intervals, rows are sampling depths. 75 % and 90 % are percentiles, max is the maximum, and 50 % is the median

Tabelle 3: Absolute Temperaturdifferenz $\Delta T$ zwischen aufeinanderfolgenden Messungen vor der Laubentfaltung (Tag 100–111). Spalten der Tabelle sind Zeitintervalle, Zeilen sind Profiltiefen. 75 % und 90 % sind Perzentile, max ist das Maximum, 50 % ist der Median

| | 5min | | | | 15min | | | | 30min | | | | 60min | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 50% | 75% | 90% | max | 50% | 75% | 90% | max | 50% | 75% | 90% | max | 50% | 75% | 90% | max |
| air | 0.15 | 0.39 | 0.95 | 12.31 | 0.29 | 0.70 | 1.66 | 12.65 | 0.48 | 1.12 | 2.43 | 14.86 | 0.80 | 1.83 | 3.70 | 14.87 |
| +65mm | 0.12 | 0.37 | 1.18 | 16.58 | 0.29 | 0.78 | 2.21 | 18.52 | 0.48 | 1.26 | 3.02 | 21.06 | 0.84 | 2.18 | 4.57 | 20.15 |
| +60mm | 0.08 | 0.22 | 0.66 | 7.75 | 0.20 | 0.54 | 1.45 | 11.29 | 0.34 | 0.92 | 2.12 | 12.14 | 0.61 | 1.62 | 3.22 | 12.93 |
| +40mm | 0.02 | 0.04 | 0.12 | 1.29 | 0.06 | 0.14 | 0.35 | 3.55 | 0.12 | 0.26 | 0.59 | 3.40 | 0.23 | 0.46 | 0.91 | 2.93 |
| +25mm | 0.02 | 0.04 | 0.10 | 1.20 | 0.05 | 0.12 | 0.30 | 2.49 | 0.10 | 0.21 | 0.51 | 2.37 | 0.18 | 0.38 | 0.77 | 2.54 |
| ±0mm | 0.01 | 0.03 | 0.10 | 1.16 | 0.04 | 0.09 | 0.26 | 1.98 | 0.08 | 0.16 | 0.40 | 2.03 | 0.15 | 0.27 | 0.58 | 2.10 |
| -50mm | 0.01 | 0.03 | 0.09 | 1.03 | 0.03 | 0.08 | 0.26 | 2.20 | 0.05 | 0.13 | 0.40 | 2.11 | 0.08 | 0.20 | 0.53 | 2.11 |

Table 4: Absolute temperature difference ΔT between successive measurements after leaf expansion (days 126–137). Columns of table are time intervals, rows are sampling depths. 75 % and 90 % are percentiles, max is the maximum, and 50 % is the median.

Tabelle 4: Absolute Temperaturdifferenz ΔT zwischen aufeinanderfolgenden Messungen nach der Laubentfaltung (Tag 126–137). Spalten der Tabelle sind Zeitintervalle, Zeilen sind Profiltiefen. 75 % und 90 % sind Perzentile, max ist das Maximum, 50 % ist der Median.

| | 5min | | | | 15min | | | | 30min | | | | 60min | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 50% | 75% | 90% | max | 50% | 75% | 90% | max | 50% | 75% | 90% | max | 50% | 75% | 90% | max |
| air | 0.10 | 0.20 | 0.36 | 5.60 | 0.21 | 0.40 | 0.65 | 6.11 | 0.37 | 0.68 | 1.08 | 6.58 | 0.69 | 1.22 | 1.85 | 6.79 |
| +65mm | 0.08 | 0.15 | 0.28 | 12.90 | 0.18 | 0.35 | 0.61 | 13.05 | 0.34 | 0.63 | 1.04 | 12.82 | 0.63 | 1.14 | 1.78 | 13.64 |
| +60mm | 0.06 | 0.13 | 0.24 | 7.31 | 0.15 | 0.30 | 0.50 | 8.32 | 0.28 | 0.54 | 0.86 | 9.38 | 0.53 | 0.95 | 1.47 | 9.40 |
| +40mm | 0.02 | 0.03 | 0.05 | 0.82 | 0.04 | 0.08 | 0.13 | 1.44 | 0.08 | 0.14 | 0.23 | 1.57 | 0.16 | 0.26 | 0.40 | 1.77 |
| +25mm | 0.01 | 0.02 | 0.04 | 0.64 | 0.03 | 0.06 | 0.10 | 1.04 | 0.06 | 0.11 | 0.17 | 1.16 | 0.12 | 0.20 | 0.29 | 1.30 |
| ±0mm | 0.01 | 0.02 | 0.03 | 0.60 | 0.02 | 0.04 | 0.07 | 0.80 | 0.04 | 0.07 | 0.12 | 0.88 | 0.08 | 0.14 | 0.21 | 1.02 |
| -50mm | 0.01 | 0.02 | 0.03 | 0.60 | 0.02 | 0.03 | 0.05 | 0.78 | 0.02 | 0.05 | 0.09 | 0.82 | 0.04 | 0.08 | 0.14 | 0.91 |

### 3.2 Tinytags

The diurnal periodicity of air temperature and changing weather conditions were also evident at the F–$A_h$ boundary, as recorded by the automatic dataloggers. In rough accordance with the profile data, temperatures ranged between 2.2 and 15.0° C (fig. 3, n = 15,100, both measurement periods pooled). However, most ranges were much smaller:

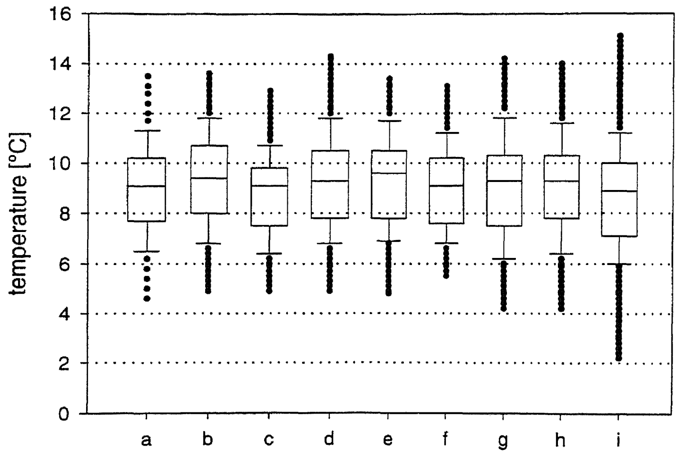


Figure 3: Temperature records from 9 microsites (a to i) at the base of the humus profile (at the boundary of F and $A_h$ horizons). Pooled data from the periods: day 94-118, and 121–148. Box edges and bar caps indicate 25/75 % and 10/90 % percentiles, respectively. Solid lines inside boxes indicate medians. Points are values lower or higher than 10/90 % percentiles

Abbildung 3: Temperaturdaten von 9 Mikro-Standorten (a bis i) an der Basis des Humusprofils (Grenze zwischen F und $A_h$-Horizont). Daten der Tage 94-118 und 121-148 vereinigt. Die Ober- und Unterkanten markieren die 25/75 %, die Abweichungslinien die 10/90 % Perzentile. Die Linien in den Boxen zeigen den Medianwert an. Punkte sind Werte außerhalb der 10/90 % Perzentile

Average 5 % and 95 % percentiles of total Tinytag data were 6.1 and 12.1° C, respectively.

Neither average temperatures nor overall temperature variability differed substantially between Tinytags (n = 15,100 measurements). Median temperatures ranged between 8.9 and 9.6° C; the data spread was similar for all Tinytags (fig. 3).

Daily temperature oscillations were generally small and rarely exceeded 4–5° C (fig. 4). There was no significant difference between median daily oscillations at the 95 % confidence level (Kruskal-Wallis test statistic = 8.41, P = 0.39, n = 52 days).

Likewise, the instantaneous measurements did not vary much between Tinytags (n=9 each 5-minute measurement). The median of ranges (highest – lowest measurement) was 1.2° C, the 95 % percentile was 2.2° C. The greatest recorded range was 4.4° C.

There was no significant correlation between humus thickness and median temperature (r = -0.55, P = 0.12), or between thickness and temperature range (r = 0.03, P = 0.94) (n = 9).

As above, the absolute difference ΔT [° C] between successive measurements was calculated at 5, 15, 30, and 60 minute intervals for the Tinytag data. In accordance with the profile measurement, temperature shifts were generally small and temperature changed very smoothly (data not shown). Differences of more than 1.0° C were rare, even for the 60 minute interval. Again, individual Tinytags behaved very similarly and the variability between them was small.

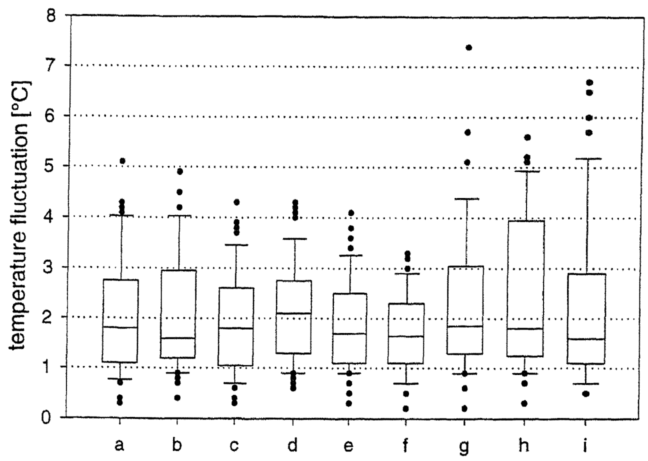


Figure 4: Ranges of daily temperature fluctuations of 9 microsites (a to i) at the base of the humus profile (at the boundary of F and $A_h$ horizons). Pooled data from the periods: day 94–118, and 121–148. Box edges and bar caps indicate 25/75 % and 10/90 % percentiles, respectively. Solid lines inside boxes indicate medians. Points are values lower or higher than 10/90 % percentiles

Abbildung 4: Spannweiten der diurnalen Temperaturschwankungen von 9 Mikro-Standorten (a bis i) an der Basis des Humusprofils (Grenze zwischen F und $A_h$-Horizont). Daten der Tage 94–118 und 121–148 vereinigt. Die Ober- und Unterkanten markieren die 25/75 %, die Abweichungslinien die 10/90 % Perzentile. Die Linien in den Boxen zeigen den Medianwert an. Punkte sind Werte außerhalb der 10/90 % Perzentile

## 4. Discussion

The results of this study corroborate FIRBAS' (1927) findings. On clear days of the leafless spring season, the L horizon exhibited great temperature extremes with wide diurnal oscillations and rapid short-term fluctuations. Peaks were much reduced after bud break; daily maxima, however, regularly exceeded 20–25° C in this period as well. I did not measure moisture content of the L horizon but found the leaves to be dry and brittle almost throughout the study period. On sunny days following rain, moist L material dries within a few hours, even after heavy precipitation (see also BABEL, 1971).

The physics of the heating of surface litter is rather simple. Dry organic matter absorbs much incoming radiation energy because of its dark color. Due to low heat capacity and low thermal conductivity, heat is concentrated on the surface and energy flow to deeper strata is minimal. Thus, the litter horizon functions as a heat shield ("protective layer", BAL, 1970). This and the high heat capacity of the underlying strata, which were moist throughout the study period, result in damped temperature fluctuations in deeper horizons.

Similar phenomena were reported from materials with the same thermal properties as forest litter. Maxima of up to 77° C surface temperature were reported from bare and dry *Sphagnum* bogs due to the low thermal conductivity of air-filled moss interstices, despite the fact that bog soils often remain frozen well into the summer (ELLENBERG, 1996). Organic mulches (hay, straw, tree bark, wood chips) are often applied in agriculture to reduce evaporation and to level temperature conditions in the mineral soil (OKE, 1987; LARSSON and BÅTH, 1996; UNGER, 1978). The latter effect can be attributed to minimal conduction of heat energy through the organic barrier.

This investigation suggests that the L horizon of deciduous forests in spring is a hostile and unpredictable environment for most soil animals that are susceptible to drought and high temperatures. This seems especially true for tiny and soft-bodied forms with limited migratory ability. Explorations of the upper horizon during moist nights or after rain may be a risky undertaking for them. It is questionable whether the L horizon is at all accessible for active life over considerable periods during the warm season. For example, sunflecks regularly heated up the humus surface in the second measurement period, when the canopy was already closed. Due to the short duration of sunflecks (median < 7 min, CANHAM et al., 1990), this warming lasted only several minutes on a specific spot, but would probably suffice to cause lethal conditions for delicate animals.

The idea of the L horizon as a hostile environment is supported by micromorphological investigations of temperate deciduous litter. BABEL (1971), BAL (1970) and ZACHARIAE (1965) reported on faeces of Oribatida, Collembola, and Enchytraeidae on leaf surfaces of the L horizon. The amounts of these remains were always very small, indicating that tiny animals have only limited access to the litter horizon and its resources during the growing season.

F and $A_h$ horizons were cool and moist throughout the study period, with minor temporal fluctuations (except for a general warming with season). They can be assumed to provide a stable and predictable environment. Diurnal fluctuations at the surface affected the temperature of deeper layers, but only to a very limited extent.

The vertical temperature variability of F and $A_h$ horizons and the horizontal variability between different microsites were surprisingly small. Thus, from a microclimatic point of view, the total depth of humus is not crucial for the fauna, as long as an overlying L layer exists. The relationship between depth of (coniferous) humus and soil temperature was described with a double exponential function by BALISKY and BURTON (1995). A 1–2 cm humus layer most effectively reduced temperature and temperature variability, whereas a humus thickness greater than 4–5 cm did not cause a further decrease.

I hypothesize that, for the humus-dwelling fauna of deciduous forests without undergrowth, it is sufficient to move only short distances in vertical direction to avoid adverse temperature and moisture conditions. This may not be easy due to the often horizontal structuring of deciduous L and F horizons and a pore space that decreases with depth. If animals move in horizontal direction, the probability of reaching cooler and moister microsites is low.

However, this hypothesis probably only applies in spring when the moisture status within horizons is more or less the same. BALISKY and BURTON (1995) found a threshold pattern of influence of humus moisture on temperature. If moisture drops below 70 %, other influential factors (predominantly humus thickness and vegetation cover) rapidly increase their influence on temperature. Under these circumstances, the spatial homogeneity of temperature and moisture of deeper strata may decrease and the humus body also be patterned in horizontal direction, resulting in a three-dimensional patchwork of moister and drier microsites (USHER, 1970) under the protective cover of the L horizon. Thus, life conditions in these strata may change from a more or less homogeneous situation in spring to a spatially patterned distribution of favorable microsites in (dry) summers.

## Acknowledgements

The Österreichische Bundesforste allowed access to the study site. E. Mursch provided part of the meteorological equipment. H. Scheiflinger patiently downloaded the encrypted weather data of the Zentralanstalt für Meteorologie und Geodynamik. E. Christian revised the manuscript. M. Stachowitsch improved the English. I thank them sincerely.

## References

ANDERSON, M. C. (1964): Studies on the woodland light climate. II. Seasonal variation in the light climate. Journal of Ecology 52, 643–663.

BABEL, U. (1971): Gliederung und Beschreibung des Humusprofils in mitteleuropäischen Wäldern. Geoderma 5, 297–324.

BAL, L. (1970): Micromorphological investigation in two moder-humus profiles and the role of the fauna in their genesis. Geoderma 4, 5–36.

BALDOCCHI, D., B. HUTCHINSON, D. MATT and R. MCMILLEN (1984): Seasonal variations in the radiation regime within an oak-hickory forest. Agricultural and Forest Meteorology 33, 177–191.

BALISKY, A. C. and P. J. BURTON (1995): Root-zone soil temperature variation associated with microsite characteristics in high-elevation forest openings in the interior of British Columbia. Agricultural and Forest Meteorology 77, 31–54.

BERG, M. P., J. P. KNIESE, J.J.M. BEDAUX and H. A. VERHOEF (1998): Dynamics and stratification of functional groups of micro- and mesoarthropods in the organic layer of a Scots pine forest. Biology and Fertility of Soils 26, 268–284.

CANHAM, C. H., J. S. DENSLOW, W. J. PLATT, J. R. RUNKLE, T.A. SPIES and P.S. WHITE (1990): Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. Canadian Journal of Forest Research 20, 620–631.

CHEN, J. and J. F. FRANKLIN (1997): Growing-season microclimate variability within an old-growth Douglas-fir forest. Climate Research 8, 21–34.

CLARK, D. B., D. A. CLARK, P. M. RICH, S. WEISS and S. F. OBERBAUER (1995): Landscape-scale evaluation of understory light and canopy structure: methods and application in a neotropical lowland rain forest. Canadian Journal of Forest Research 26, 747–757.

ELLENBERG, H. (1996): Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht. 5. Auflage. Ulmer, Stuttgart.

FIRBAS, F. (1927): Über die Bedeutung des thermischen Verhaltens der Laubstreu für die Frühjahrsvegetation des sommergrünen Laubwaldes. Beihefte zum Botanischen Zentralblatt 44, 179–198.

FRANSSILA, M. (1960): On the measurement of soil temperature in forests and swamps. Finnish Meteorological Office Contributions 52, Helsinki.

GREEN, R. N., R. L. TROWBRIDGE and K. KLINKA (1993): Towards a taxonomic classification of humus forms. Forest Science Monograph 29, 1–49.

HOKKANEN, T. J., E. JÄRVINEN and T. KUULUVAINEN (1995): Properties of top soil and the relationship between soil and trees in a boreal Scots Pine forest. Silva Fennica 29, 189–203.

HUTCHISON, B. A. and D. R. MATT (1977): The distribution of solar radiation within a deciduous forest. Ecological Monographs 47, 185–207.

KILLHAM, K. (1994): Soil Ecology. Cambridge University Press, Cambridge.

LARSSON, L. and A. BÅTH (1996): Evaluation of soil temperature moderation and moisture conserving effects of various mulches during a growing season. Acta Agriculturae Scandinavica B, Soil and Plant Sciences 46, 153–160.

MCINNIS, B.G. and M. R. ROBERTS (1995): Seedling microenvironment in full-tree and tree-length logging slash. Canadian Journal of Forest Research 25, 128–136.

OKE, T .R. (1987): Boundary Layer Climates. 2nd ed. Routledge, London.

SPITTLEHOUSE, D. L. and R. J. STATHERS (1990): Seedling Microclimate. British Columbia Ministry of Forests, Victoria.

TOPP, W. (1981): Biologie der Bodenorganismen. Quelle & Meyer, Heidelberg.

UNGER, P.W. (1978): Straw mulch effects on soil temperatures and Sorghum germination and growth. Agronomy Journal 70, 858–864.

USHER, M. B. (1970): Pattern and seasonal variability in the environment of a Scots Pine forest soil. Journal of Ecology 58, 669–679.

XU, M., J. CHEN and B. L. BROOKSHIRE (1997): Temperature and its variability in oak forests in the southeastern Missouri Ozarks. Climate Research 8, 209–223.

ZACHARIAE, G. (1965): Spuren tierischer Tätigkeit im Boden des Buchenwaldes. Parey, Hamburg.

## Corresponding author

**Mag. Dr. Alexander Bruckner**, Institute of Zoology, University of Agricultural Sciences Vienna, Gregor-Mendel-Str. 33, A-1180 Vienna, Austria

Eingelangt am 27. Oktober 1998
Angenommen am 22. Jänner 1999